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Prey handling and feeding habits of the snail predator *Licinus depressus* (Coleoptera, Carabidae)

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Abstract

Carabid beetles of the tribe Licinini use their asymmetric mandibles to open the shells of land snails. Prey handling of large snails has been described in a few Licinini species. We observed for the first time how a male of *Licinus depressus* (Paykull, 1790) opens the shells of small prey snails (*Chondrina arcadica* (Reinhardt, 1881)) and eats their soft bodies. The beetle holds the conical snail shell with its forelegs and breaks the wall of the right-hand coiled shell. In doing so, the beetle rotates the shell counter-clockwise opening it stepwise along the dorsal part of the whorls towards the apex. After some bites, the beetle interrupts the opening process and begins to feed on the snail's soft tissue. Then the beetle continues to break up the shell, shortly after which there is another feeding phase. The alternating sequence of shell breaking and feeding ends after 2 to 2.5 whorls when the beetle can no longer hold the prey's remaining intact shell. We compare this previously unknown way of prey handling with the reported predatory behaviour in large snails by other Licinini species. Our observations confirm the high plasticity of predatory behaviour in Licinini beetles.

Key Words

Insect, feeding behaviour, asymmetrical mandibles, shell coiling, gastropod, predator-prey interaction

Introduction

Asymmetric morphology and function have been described in several groups of insects (Palmer 1996). Carabid beetles of the tribe Licinini have asymmetric mandibles (Forsythe 1983; Ball 1992). Their mouthparts are adapted to a specialized diet, mainly land snails. The mandibles crush the prey's shell to reach the soft tissues inside (Erwin et al. 2015; Hayashi and Sugiura 2021). However, the Licinini beetles' feeding behaviour has only been studied in a few species. Adult individuals of *Badister pictus* Bates, 1873 begin their attacks by breaking the outer lip of the prey snail's dextral (right-handed coiled) shell, which lies on the ground (Hayashi and Sugiura 2021). The left and the right mandible are always placed against the external and internal shell wall, respectively. When the outer lip of a shell is broken by biting, the beetle breaks open the shell further along the dorsal part of the whorls towards the apex (Hayashi and Sugiura 2021). During the whole process the beetle fixes the shell with its forelegs and moves around the prey snail. A very similar cracking of snail shells has been described in three *Licinus* species (*L. cassideus* (Fabricius, 1792), *L. hoffmannseggi* (Panzer, 1797), *L. italicus* Puel, 1925; Brandmayr and Zetto Brandmayr (1986)). Through repeated bites, the beetles open the first whorl of the shell and – in most cases – a part of the second whorl (420° and more; figs 2, 3 in Brandmayr and Zetto Brandmayr (1986)). Breaking the shell wall takes four or more hours. The actual feeding begins after the shell wall has broken through at least a whole whorl. Depending on the size of the snail, it takes 12 hours or more to consume

the prey's soft tissue (Brandmayr and Zetto Brandmayr 1986). However, the soft tissue of the inner whorls is never consumed. In the cases described, the prey snail was at least half the size, and often significantly larger, than the predatory beetle (Brandmayr and Zetto Brandmayr 1986; Hayashi and Sugiura 2021).

During field work on the population dynamics of land snails in the grassland Great Alvar on the Baltic island of Öland, Sweden, we found a male of *Licinus depressus* (Paykull, 1790) feeding on a small snail under a flat piece of limestone. The prey was a *Chondrina arcadica* (Reinhardt, 1881) (formerly *Chondrina clienta*), a snail with a cylindro-conical shell that has about seven moderately convex whorls and is 5–6 mm high in fully-grown individuals (Fig. 1). Under the same piece of stone we found several shells of *C. arcadica* showing typical traces of beetle predation. We captured the beetle in order to investigate its shell-breaking and feeding behaviour in the laboratory under near-natural conditions.

Licinus depressus is considered an obligate snail predator, at least as a larva (Lindroth 1949; Kinnunen 1996). However, its predatory behaviour has never been documented. Here we show how *L. depressus* opens the shells of small prey snails and eats their soft bodies. We compare this previously unknown way of prey handling with the reported predatory behaviour in large snails by other species of the tribe Licinini.

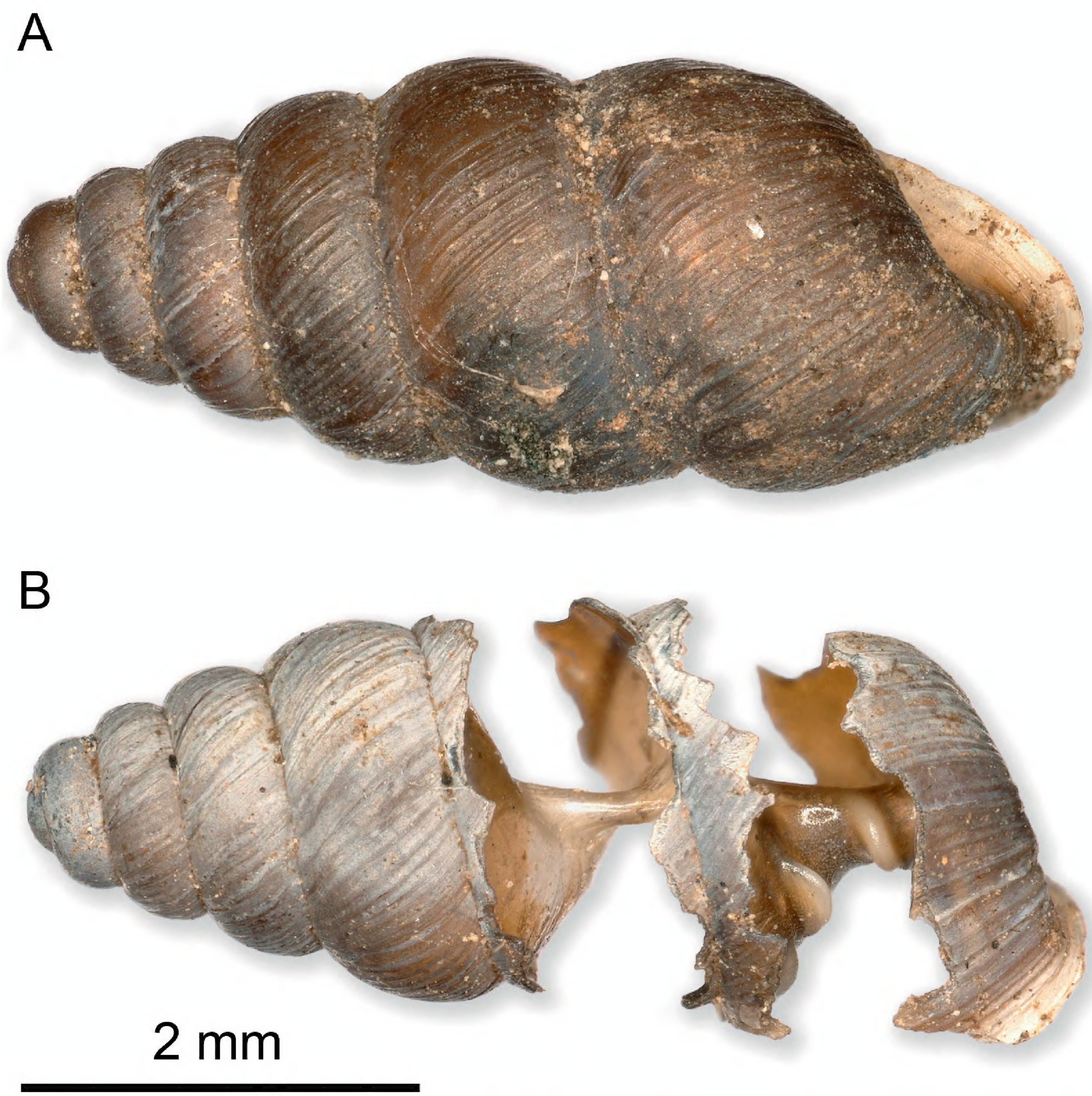

Figure 1. Intact shell of *Chondrina arcadica* (**A**), and shell opened by *Licinus depressus* (**B**). The bite marks of the mandibles are clearly visible. Photo: José D. Gilgado.

Material and method

The xerophilous *Licinus depressus* (body length 9.5–11.8 mm) occurs in Central and Eastern Europe, in Southern Scandinavia, on the British Islands, and in Russia (GBIF 2023). In Switzerland, the xerophilous species has been reported mainly in the Jura mountains and in valleys of the Alps (cantons of Valais and Grison; Info fauna 2023). Individuals of *L. depressus* are found scattered in calcareous areas with dry, sandy or gravelly soils at somewhat shaded sites in grasslands, on overgrown dunes, and in dry forests (Lindroth 1986).

We captured a male of *L. depressus* feeding on a snail under a piece of limestone at the foot of a stone pile in the grassland Great Alvar (56.61565°N, 16.49963°E) on the Baltic island of Öland, Sweden, on 8 October 1995. *Licinus depressus* has been found previously in the Great Alvar on Öland (Lundberg 1983). The beetle was kept in a transparent plastic box (14 × 10 × 7 cm in size) containing a flat piece of limestone. The bottom of the container was covered with moistened paper towel. We collected adult *C. arcadica* as prey from the beetle's place of origin. *Chondrina arcadica* is abundant on rock habitats (limestone pavements, stone walls, piles of stones) in the Great Alvar (Baur 1988; Baur and Baur 1995). We offered the beetle a prey snail on each of four consecutive days. In each case, the active snail was placed on the moistened stone. We observed the beetle's prey handling and feeding under dimmed light conditions.

We photographed the shell of both an intact and a cracked shell of *C. arcadica* using a digital microscope Keyence VHX-6000 (Keyence Corporation, Osaka, Japan). Based on photographs, A. Coray made a drawing of the typical prey handling of *L. depressus*. The specimen of *L. depressus* examined has been deposited in the Natural History Museum of Basel, Switzerland.

Results

Within a few minutes, the *L. depressus* male found the prey snail. The beetle grabbed the snail with its forelegs while maintaining a stable position with its middle and hind legs (Fig. 2). The snail is held at the first and second whorl, with the apex of the shell pointing towards the back of the beetle. After breaking the outer lip of the dextral (right-hand coiled) shell, the beetle rotated the conical shell 20–30 degrees counter-clockwise and bit again, opening the shell stepwise along the dorsal part of the whorls towards the apex. The cracking of the shell was clearly audible. After six to eight bites (approximately 120 degrees of a whorl), the beetle interrupted the opening process and began to pull the snail's soft tissue out of the opened shell (Fig. 3). While feeding, the beetle continued to hold the shell with its forelegs and did not change its position. Then the beetle continued to break up the shell, shortly after which there was another feeding phase. The alternating sequence of shell breaking and feeding ended after 2 to 2.5 whorls (out of a total of 6–7 whorls) when the beetle could no longer hold the remaining unbroken shell of the prey (Fig. 1). In this way the beetle was able to consume about two thirds of the snail's soft body. In the four observed cases, prey handling and feeding was rather rapid with a total duration of 2.5 to 4 minutes.

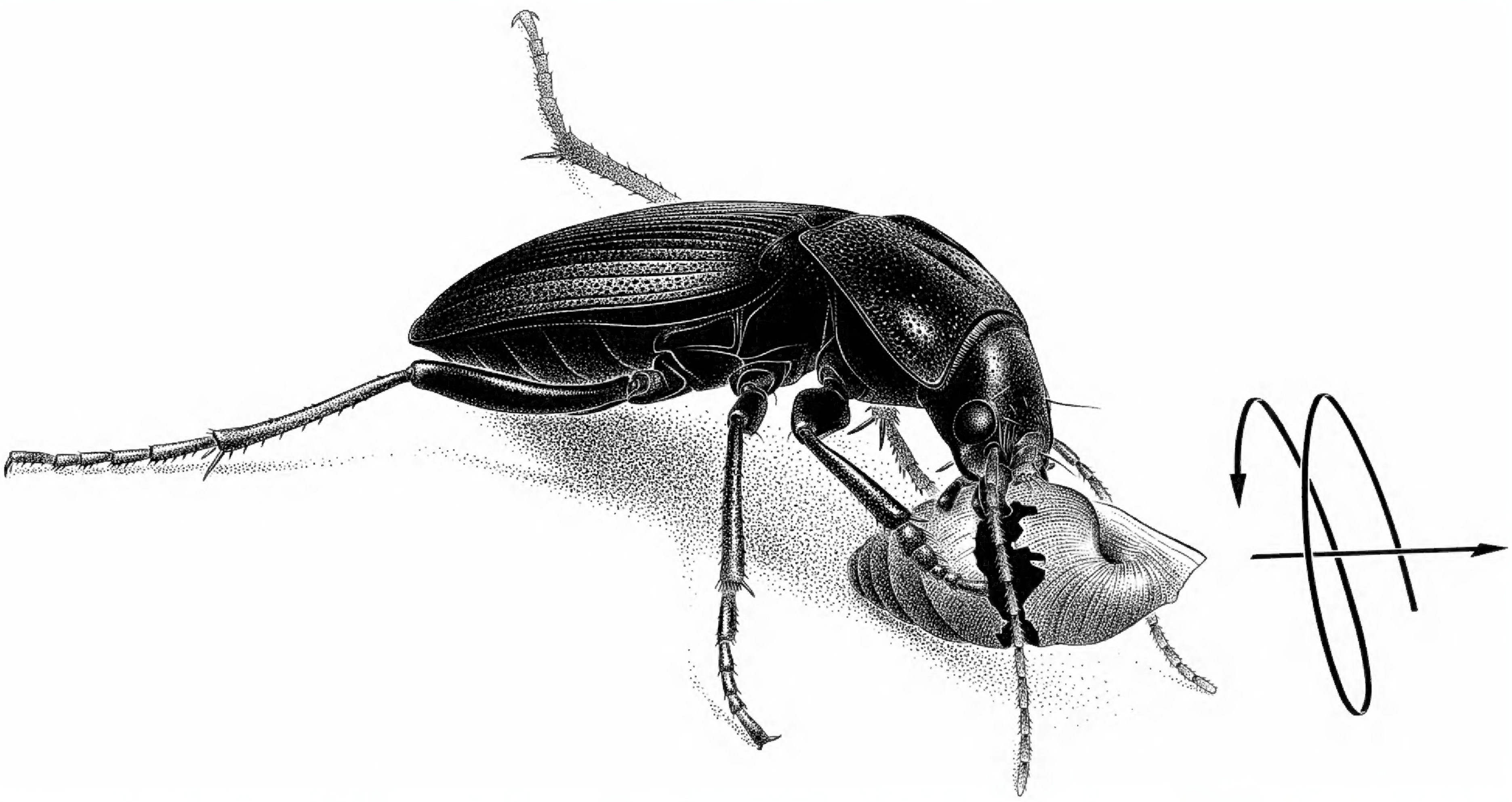

Figure 2. The predatory beetle *Licinus depressus* holds onto a prey snail (*Chondrina arcadica*) with its forelegs and breaks through the shell wall with its asymmetrical mandibles. Drawing: Armin Coray.

Figure 3. The predatory beetle *Licinus depressus* interrupts the opening process of the shell and begins to feed on the soft tissue of the prey snail. Photo: Bruno Baur.

Discussion

The handling and feeding behaviour described here differs significantly from previous descriptions of this behaviour in other Licinini species. In the reported cases, the prey snail was, in relation to the size of the predatory beetle, significantly larger, often exceeding the predator size (Brandmayr and Zetto Brandmayr 1986; Hayashi and Sugiura 2021). Any holding of the prey with the forelegs was therefore not possible. Large prey snails are held on the ground while the predatory beetle moves around the shell, gradually opening it. In all detailed descriptions of shell crushing, the beetle only began to feed after finishing the opening process, which itself lasted 12 and more hours (Brandmayr and Zetto Brandmayr 1986; Hayashi and Sugiura 2021). In contrast, *L. depressus* held the prey snail with its forelegs during both shell breaking and feeding, alternated between shell breaking and feeding several times, and prey handling and feeding lasted only a few minutes. On the other hand, what is common to both forms of prey handling is that a considerable part of the snail's soft tissue (approximately one third) is not eaten. Possible explanations for this are that the inner whorls of the shell are too narrow to open them with the mandibles, or that the further energy intake from the additional food is low in relation to the handling time. In addition, in the case of *L. depressus*, the beetle is no longer able to hold the partially opened shell with its forelegs.

It is interesting to compare the food intake of the two forms of prey handling. Shell length-biomass relationships are a reliable method to estimate the dry weight of gastropod soft bodies (Calow 1975; Hawkins et al. 1997). According to Brandmayr and Zetto Brandmayr (1986), a *Licinus italicus* female devoured one snail (shell diameter 13 to 20 mm) every five days. Snails of this size range have a soft body dry weight of 13 to 27 mg compared to 3 mg of a 5.5 mm long *Chondrina arcadica*. This indicates that a beetle would need to eat one to two *C. arcadica* per day to have the similar food intake as a beetle that chooses large snails as prey. In the Great Alvar, *C. arcadica* occurs in high densities, mainly on stone walls, in stone piles and on limestone pavements (Baur and Baur 1990). Large snails are rare in this grassland, an exception being *Helicigona lapicida* (Linneus, 1758) in abandoned limestone quarries (Baur and Baur 2006). It is therefore not surprising that *L. depressus* frequently eats small prey snails, such as *C. arcadica* and *Cochlicopa lubrica* (O. F. Müller, 1774), which can be found in the grassland with little search effort (B. Baur, unpubl. data).

Specific external or internal traces on shells left by the predators indicate who killed the snail (birds, rodents, beetles, or parasitoid flies; Němec and Horsák 2019). In limestone steppes in Slovakia and the Czech Republic, beetles have been found to be the most common predators of snails (Němec and Horsák 2019). Similarly, among numerous empty shells collected from dry grasslands in the Swiss Jura mountains, shells of similar size and shape such as *C. arcadica* (*C. lubrica*, *C. lubricella* (Rossmässler, 1834), *Abida secale* (Draparnaud, 1801)) with traces of Licinini predation have been regularly found (Boschi

and Baur 2008). In addition, empty shells of *Chondrina avenacea* (Bruguière, 1792) and *A. secale* with the same feeding marks were regularly found in the Alps (B. Baur, unpubl. data). However, it is not possible to assign shells to a specific beetle species using traces from predation.

Our observations are based on one individual and five predation events (one field observation, four laboratory observations). However, the numerous empty snail shells found in the field with these specific feeding marks (Fig. 1) indicate that this form of prey handling occurs regularly in *L. depressus* and possibly other Licinini beetles. However, their prey handling and feeding behavior under stones and in the dense ground vegetation are hardly observed.

Land snails exhibit a great diversity of shell forms (Kerney and Cameron 1979). Many of the shell traits (e.g., whorl number and size, aperture shape and size, shell shape, shell thickness and size) are adaptive responses to abiotic ecological factors, while some shell traits (e.g., aperture shape and size, shell size, shell wall thickness, and shell coiling direction) are known to provide a selective advantage when faced with predation (Goodfriend 1986; Liew and Schilthuizen 2014). Land snails are prey for different predators and are accordingly exposed to different selection pressures (Schilthuizen et al. 2006; Němec and Horsák 2019).

With its asymmetrical mandibles and particular behaviour of holding the small conical shell with its fore-legs, *L. depressus* can only open right-handed coiled shells, but not left-handed coiled shells (Fig. 2). *Balea perversa* (Linnaeus, 1758) is a snail of similar size to *C. arcadica* and both species coexist in stony habitats of the Great Alvar (Baur and Baur 1990). However, we have never found a shell of *B. perversa* with traces of beetle predation in the Great Alvar. In contrast to *C. arcadica*, shell coiling in *B. perversa* is left-handed (sinistral). The unusual (rare) shell coiling may give this species an advantage against *L. depressus* attacks. This argument is supported by other studies showing that predatory insects with asymmetrical mandibles specialize in snails with a specific shell coiling direction (Hoso and Hori 2008).

Brandmayr and Zetto Brandmayr (1986) proposed high plasticity of predatory behaviour in Licinini. For example, *Licinus cassideus latus* opened shells of juveniles *Helix aspersa* (= *Cornu aspersum* (O. F. Müller, 1774)) with a shell diameter of 7–12 mm by breaking the whorls as described above. In individuals with a shell diameter larger than 20 mm, however, the beetle simply entered through the shell aperture and began feeding (Brandmayr and Zetto Brandmayr 1986). Our observations on how to deal with small prey snails expand the repertoire of known predatory behaviour. At the same time, our observations confirm the high plasticity of predatory behaviour in Licinini beetles.

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